

Ecological implications of intertidal mariculture: observed differences in bivalve community structure between farm and reference sites

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Summary

1. Despite recent growth in shellfish aquaculture in British Columbia, Canada, the impacts of common practices on non-target species are poorly understood. Two practices employed on clam farms to increase production of the exotic clam *Venerupis philippinarum* include the addition of juvenile 'seed' clams to the sediment and covering seeded clam beds with protective netting, ostensibly to exclude large mobile epibenthic predators.
2. We expected the effects of predator exclusion to be most evident among other bivalves, which made up more than 80% of the infaunal macrobenthos at all sites surveyed. A field study across three regions collected infaunal bivalve density and biomass data. We compared species richness, composition and abundances of communities between clam farms and reference sites, paired on the basis of physical characteristics such as sediment type, slope and aspect.
3. *Venerupis philippinarum* was the only species found in higher abundance on farm sites in low intertidal areas (227 ± 241.6 clams m^{-2} , $P = 0.02$; 872.9 ± 792.9 g m^{-2} , $P = 0.037$). Farmed sites showed no difference in mid-intertidal areas, nor in density of the other 25 bivalve species, although an increase would be expected if netting excluded important predators. Although statistically non-significant, there were indications that biomass of species other than *V. philippinarum* may have been lower on farm sites.
4. Bivalve species composition was not significantly different between farm and reference sites. Nevertheless, farm sites were more similar to each other as a group than reference sites, leading to a loss of regional distinctness that was evident among reference sites.
5. *Synthesis and applications.* Our findings support the hypothesis that predation and competition play minor roles in structuring communities in soft-bottomed environments. Given the potential for cumulative effects of seeding and netting at large scales, a precautionary approach is recommended in future development of intertidal clam aquaculture.

Key-words: bivalves, clam aquaculture, community structure, predator exclusion, *Venerupis philippinarum*

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Introduction

Bivalves are an important component of many soft-bottom marine communities and play a major role in

cycling nutrients between sediments and the overlying water column (Dame 1996). Infaunal bivalves (clams) also serve as an important food source for marine predators, including crabs (Virnstein 1977; Spencer, Edwards & Millican 1992), worms (Bourque, Miron & Landry 2001), fish (de Goeij *et al.* 2001), snails (Peitso *et al.* 1994), birds such as sea ducks (Jamieson *et al.* 2001) and humans.

Clam aquaculture in British Columbia (BC), Canada, began experimentally in Baynes Sound (see Fig. S1 in

the supplementary material) in 1969, with formal licensing of intertidal sites exclusively for shellfish aquaculture commencing in 1991 (Jamieson *et al.* 2001). Clam production has since increased to more than 1500 tonnes, valued at more than 7 million dollars, and represents half of the province's total shellfish aquaculture industry (see Fig. S2 in the supplementary material), which occupied 2800 ha of sites in 2003 (BC Ministry of Agriculture and Lands 2004).

The commercially dominant species in the industry is the non-native manila clam *Venerupis philippinarum* (Harbo 1997), introduced to BC with the Japanese oyster seed *Crassostrea gigas* (Quayle & Bourne 1972). *Venerupis philippinarum* production is commonly enhanced on farm sites by adding hatchery-reared juveniles to intertidal sediments ('seeding') followed by placing nets over the seeded substrate to protect juvenile clams from predation (Jamieson *et al.* 2001). Clams are harvested year-round using hand-raking, after reaching a minimum length of 38 mm 2–4 years after seeding, depending on growing conditions at the site (Jamieson *et al.* 2001).

Protective nets include a variety of plastic netting as well as woven rope, with apertures of 1.25 cm and 3.5 cm, respectively. Nets are applied in one or two layers, then anchored with large rocks or steel posts. The nets frequently attract macro-algae and other 'bio-fouling' organisms, which must be removed manually before large amounts reduce circulation of water and food particles to the sediment surface (Jamieson *et al.* 2001; Spencer, Kaiser & Edwards 1996, 1997).

In the UK similar nets were used to exclude crabs (Spencer, Edwards & Millican 1992), and in BC they are also used to exclude scoters (diving ducks *Melanitta* spp.), fish and other large predators. The British Columbia Shellfish Growers' Association (BCSGA) (BCSGA 2004) claims that, without such predator exclusion, approximately 40% of clams would be lost to predation, in addition to the 40–50% loss expected even under such nets. Relative predation intensity may be variable within BC, although fish, crabs, diving ducks and other predators are abundant in many areas of coastal BC, often in areas that may coincide with shellfish aquaculture sites (Jamieson *et al.* 2001).

This research addressed the following questions. (i) Are bivalve species more or less abundant on farm sites, relative to paired reference sites, and is there evidence of competitive exclusion within predator refuges offered by clam netting? (ii) Is bivalve community structure (species richness, evenness, composition) different between paired sites? In particular, are native bivalve species affected by practices used to produce a single non-native bivalve species?

Materials and methods

STUDY AREA AND SITES

All field sampling occurred at sites in southern coastal BC, within three distinct regions: Barkley Sound, Baynes

Sound and Desolation Sound (Okeover Inlet) (see Fig. S1 in the supplementary material). All are areas of shellfish aquaculture development, with different overall activity levels and unique geographical characteristics (for Baynes Sound details see Jamieson *et al.* 2001).

A paired design allowed comparisons that accounted for differences between pairs, to help control unknown variability that has often confounded intertidal experiments (Sewell 1996; Richards, Huxham & Bryant 1999; Peterson *et al.* 2001). Because predator exclusion netting was a common practice on clam farms, this study presented an opportunity to examine community responses at a spatial scale larger than most published experiments. Both seeding and netting were present together on farm sites, therefore the relative effects of these two practices could not be separated.

The most important difference between each farm and reference site within pairs was the application of seeding and netting to the farm sites. Reference sites were selected to match a paired farm site as closely as possible with respect to sediment type, slope, size and wave exposure (see Fig. S1 in the supplementary material; site characteristics are listed in Table 1).

Farm sites were selected based on permission from lease owners and availability of a suitable reference site. This type of observational sampling compared the current state of farm sites to existing reference sites, integrating changes in response to combined aquaculture practices over the site's entire history (1–10 years; Table 1). This study did not include the largest clam aquaculture leases currently active in BC; the results only apply at the scale of the farm sites that were sampled.

Two additional sites, B3 reference and A3 farm, were both matched to sites with seeding but without netting (seeding on A3 reference site became apparent after sampling). These mismatched sites could not be used in paired analyses but were included in multivariate analyses, which did not take pairing into account.

Two 'pre-farm' sites sampled, A5 and D3, had been selected for future clam aquaculture but no aquaculture activity had started prior to sampling. These sites were included as additional reference sites in the multivariate analyses.

SAMPLING METHODOLOGY

Sampling methods were based on those developed by Gillespie & Kronlund (1999) for intertidal clam sampling but adapted for sampling a broader range of species. All field data and samples were collected during daytime low tides between May and August 2003. Only infaunal bivalve data from the field study are reported here. More than 80% of infaunal macrobenthos individuals at all sites were infaunal bivalves (clams). Although interactions between bivalves and other burrowing species, such as mud shrimp (e.g. *Upogebia pugettensis*), have been reported as important (Smith & Langdon 1998), non-bivalves comprised such a small

Table 1. Characteristics of study sites, including sample size (number of quadrats sampled). Site pairs are labelled by region (A, Baynes Sound; B, Barkley Sound; D, Okeover Inlet, Desolation Sound) and a number

Region	Site	Tide stratum	Type	Size (m ²)	No. years netted	Range mean particle size (mm)	Sediment type (visual)	No. quadrats sampled				
Baynes Sound	A1	Low	Farm	500	4	0.403–1.208	Sand, silt	12				
			Reference	11638					0.285–0.526			
	A2	Low	Farm	3650	4	0.889–1.636	Gravel, sand	12				
			Reference	8575					0.222–0.827			
			Farm	1400					2	1.236–1.844	Sand, silt	18
			Reference	1400								
*	A3	Mid	Farm	1120	6	1.419–2.581	Gravel, sand	18				
			Reference	21750					0.369–1.967			
Barkley Sound	B1	Low	Farm	1158	1	1.418–3.747	Gravel, sand	18				
			Reference	800					2.045–2.988			
	B2	Low	Farm	1190	1	0.589–2.512	Gravel, sand	18				
			Reference	501					0.840–1.187			
			Farm	2035					10	0.544–1.040	Gravel, sand	18
			Reference	739								
Desolation Sound	D1	Mid	Farm	449	7	0.534–3.228	Gravel, sand	18				
			Reference	342					0.732–1.619			
	D3	Low	Pre-farm	451	–	0.512–3.416	Gravel, sand	12				
			Reference	623					1.780–6.211			
			Pre-farm	449					–	1.420–2.763	Gravel, sand	12
			Reference	198								

*Sites that did not fit the overall paired treatment scheme and were excluded from univariate paired analyses but included in multivariate analyses.

and inconsistent portion of the communities sampled in our study that we expected community effects from these interactions to be negligible. The sites in our study were composed of relatively coarser grains (Table 1) than mudflats in other areas where burrowing shrimp are more common.

Sites were stratified by tide height; areas between 1 and 2 m above chart datum (long-term mean of daily lowest low-water level) were classified as 'low', and areas above 2 m, to the top of netted areas, were classified as 'mid'. The highest points sampled were at 2.7 m above chart datum. Stratum boundaries were shifted 0.5 m lower in Barkley Sound to accommodate lower average tides than the other regions. Reference beaches were laid out to match the paired farm site according to surface area and tidal range, within patches of similar sediment type.

Quadrats were placed randomly within each stratum at each beach (see Table 1 for sample sizes). A stainless steel square frame (0.5 × 0.5 × 0.3 m deep) was inserted into the substrate and all sediment to a depth of 20 cm was removed by shovel and sifted through a 6-mm mesh. A subsample of sediment (0.25 × 0.25 m) within the top-right corner of each quadrat was passed through a 1-mm mesh sieve under the 6-mm sieve, to capture smaller individuals. Large amounts of sediment retained in each sieve were also hand-sifted to locate organisms.

Infaunal bivalves were identified in the field to the lowest taxonomic level possible, usually species, using field guides (Harbo 1997; Sept 1999). Difficult or unknown specimens were stored in ethanol for later identification using additional resources (Kozloff 1983; Kozloff & Price 1987) or invertebrate experts (e.g. Bamfield Marine Sciences Centre, Bamfield, Canada). For one-third of quadrats, blotted wet weight (0.1 g), and length (mm) of individual bivalves were recorded. All bivalves were returned to the sediment post-sampling.

Sediment type was assessed qualitatively by recording the two most abundant particle size classes present (after Wentworth 1922). Sediment cores (5 cm diameter × 10 cm deep), from four randomly selected quadrats at each site, were processed in the laboratory for particle size distribution. Each sediment sample was wet sieved (stacked 2-mm, 0.25-mm, 0.063-mm mesh sizes) and each size fraction dried and reweighed separately. The 'mud' fraction (< 0.063 mm) was determined by subtraction of all other fractions from a sample's total dry weight. The range of particle size geometric means over each site is reported in Table 1.

STATISTICAL TREATMENT AND ANALYSIS

For each quadrat, counts of bivalves from the 0.25 × 0.25-m subsample were multiplied by 4 to normalize by

area, and added to counts of larger individuals from the 0.5 × 0.5-m quadrat. Bivalve species were grouped by primary feeding mode: all species were either obligate suspension feeders or facultative surface deposit feeders. For each estimate, paired *t*-tests were used to determine consistent differences between farm and reference sites. For density and biomass data, quadrat values were averaged over each site. Because such site means were estimates themselves, differences were weighted (Sokal & Rohlf 1981) using the inverse of a pooled estimate of standard error within each site pair. All univariate statistical tests were computed using a pooled estimate of variance across the low and mid strata, to allow tests for differences between strata, with significance at 0.05.

Species richness estimates [first-order jack-knife, abundance-coverage estimator (ACE) and Incidence-based Coverage Estimator (ICE)] and diversity indices (Simpson's Evenness and Shannon-Wiener diversity) were computed with the EstimateS software program (Colwell 2005). For this study, estimators were selected based on their ability to discriminate between estimates (high precision), rather than estimating the true number of species (reducing bias).

Both the jack-knife and ICE estimators are incidence-based, and therefore potentially sensitive to changes in spatial distribution or patchiness (Brose, Martinez & Williams 2003; Foggo *et al.* 2003). A decrease in patchiness may result in a lower estimate of species richness, independent of any actual change in the number of species present at a site. This was the primary reason for also comparing sites using ACE.

Sites were also compared with respect to community evenness, using Simpson's evenness index, and information-theoretic species 'diversity', calculated using the Shannon-Wiener function (Krebs 1999). Indices such as the Shannon-Wiener function are composite measures incorporating both richness and evenness. Changes in such a composite measure are difficult to interpret, unlike separate measures of richness and evenness. The Shannon-Wiener function was included to allow comparison with other studies.

Multivariate comparisons of bivalve communities were performed using PRIMER software (Clarke & Gorley 2004). Bivalve counts and weights were converted to an average density and biomass per square metre, to standardize for different sample sizes. Density and biomass data were analysed separately. Similarity matrices were calculated using the Bray-Curtis index of similarity (Legendre & Legendre 1998) on fourth-root transformed data, which was used to draw non-metric multidimensional scaling (MDS) plots.

Analysis of similarity (ANOSIM) was also performed on the same similarity matrices. This procedure is a multivariate non-parametric test of differences between groups defined *a priori*, analogous to analysis of variance (ANOVA) (Clarke & Green 1988; Clarke 1993). A maximum of 999 permutations was used randomly from a set of all possible permutations in any test. The result was a probability of observing a relative dissimilarity

between groups as large as that in the data, assuming the null hypothesis that communities were assigned to groups randomly. The null hypothesis could also be stated as 'no group differences' (Clarke & Green 1988).

We tested for differences among types (farm or reference) and tide height strata (low or mid intertidal) in a two-factor crossed analysis, which tested for differences in each factor averaged over all levels of the second factor (Clarke 1993). Some regions did not include sites in all tide height strata, so some combinations of region and stratum did not exist. In the absence of significant differences for any other factor, regional differences would indicate that community structure is more strongly determined by local factors that vary by region, as opposed to the broader factors of tide height and farming practices.

Sites sampled under pre-farming conditions (A5 and D3) were included in these analyses as additional reference sites. Sites that had been seeded but not netted (A3 reference and B3 farm) were excluded from the multivariate analyses.

Results

DENSITY AND BIOMASS

Venerupis philippinarum accounted for the majority of clam density (Fig. 1) and biomass (Fig. 2) at all farm sites plus some reference sites. Clam abundance and biomass were abnormally higher at D2 reference site than any other site sampled in this study. These high abundances may have been the result of a permanent closure of shellfish harvesting at the site, or the result of enhanced nutrient inputs from unknown sources. This

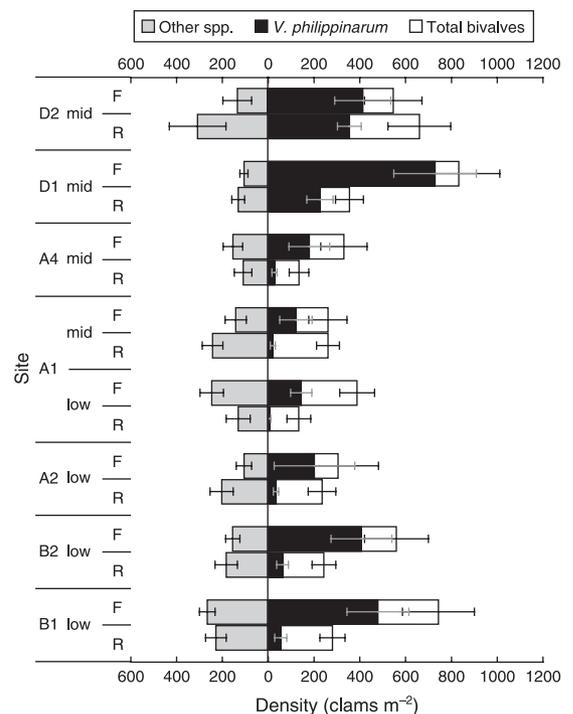


Fig. 1. Mean clam density (individuals m⁻²) at field study sites. Error bars represent 95% confidence intervals about each mean.

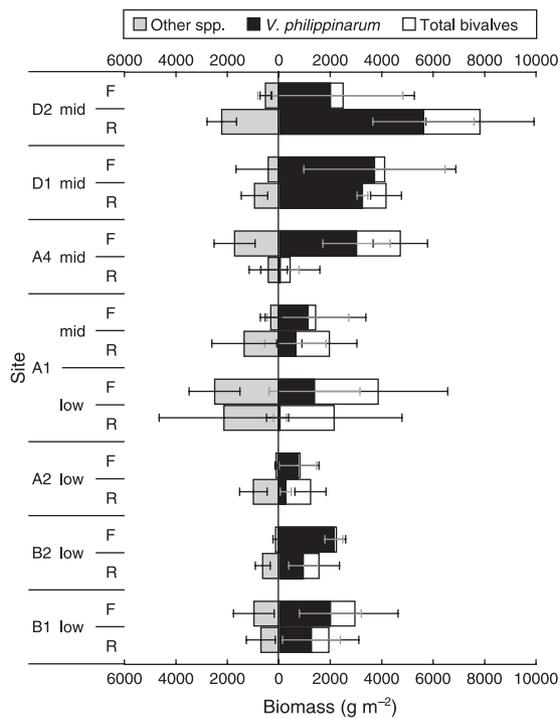


Fig. 2. Mean clam biomass (g m^{-2}) at field study sites.

site pair was also highly influential in the pairwise analysis of biomass values and was excluded as an outlier.

We found no significant difference in any abundance of clams in the mid intertidal between farm and reference sites ($P > 0.05$; Table 2). Total clam density was significantly greater on farm sites, but only in the low stratum ($P = 0.03$). *Venerupis philippinarum* occurred at higher densities and biomass on farm sites in the low stratum ($P = 0.02$). The average difference in *V. philippinarum* density (227.0 ± 176.4) was approximately the same as the observed difference in total clam

density (279.6 ± 241.6) in the low stratum. Total clam density and biomass, excluding *V. philippinarum*, were not significantly different between farm and reference sites, although biomass of other clams was on average lower at farm sites. All clam species encountered were either obligate suspension feeders or facultative deposit feeders (also capable of suspension feeding) but neither feeding guild, excluding the filter-feeding *V. philippinarum*, showed a significant difference between farm and reference sites (Table 2).

The volume occupied by clams was calculated by treating each clam as a sphere with diameter equal to its observed length. The total volume of clams in quadrats was averaged for each site and converted to a percentage of the volume of a typical quadrat ($50 \times 50 \times 20$ cm). Clams occupied an average of 2.0% of quadrat volume, ranging between less than 0.01% and up to 13.2% at individual quadrats. The most conservative estimate would be to assume a two-dimensional environment, with clams as squares with sides equal to their length, in which case clams occupied an average of 20% of available space, ranging from 0.07% to 130% (more than could fit on the surface) at individual quadrats.

UNIVARIATE COMMUNITY INDICES

Twenty-six bivalve species were observed in total on all sites, including four unique unidentified species, but there were no significant differences in the number of bivalve species, evenness and diversity between farm and reference sites (Table 3). Values for individual sites are presented in Table S1.

MULTIVARIATE ANALYSIS

Stress values for MDS plots of density data (0.18, 0.19; Fig. 3) were considered acceptable, although some

Table 2. Results of weighted paired analyses of bivalve abundance including mean difference (farm–reference, F–R) \pm 95% confidence interval (CI) (with degrees of freedom) for each estimate. Mean differences significantly different from zero (two-tailed) are highlighted in bold

Test	Low stratum		Mid stratum	
	Mean difference (F–R) \pm 95% CI	P-value	Mean difference (F–R) \pm 95% CI	P-value
Density (individuals m^{-2}) (d.f. = 6)				
Total clams	279.6 ± 241.6	0.030	131.8 ± 237.7	0.224
<i>Venerupis philippinarum</i>	227.0 ± 176.4	0.020	162.8 ± 185.7	0.076
Other clams (<i>V. philippinarum</i> excluded)	-2.1 ± 100.5	0.960	-34.1 ± 97.0	0.422
Suspension-feeding clams	-176.18 ± 573.4	0.481	-201.73 ± 745.9	0.533
Deposit-feeding clams	-84.3 ± 332.0	0.557	-32.0 ± 379.1	0.843
Biomass (g m^{-2}) (d.f. = 5)*				
Total clams	444 ± 1698.0	0.531	1089.7 ± 2812.0	0.365
<i>Venerupis philippinarum</i>	872.9 ± 792.9	0.037	1201.3 ± 1449.5	0.086
Other clams (<i>V. philippinarum</i> excluded)	-452.3 ± 852.1	0.231	-226.1 ± 1228.4	0.656
Suspension-feeding clams	17.9 ± 48.2	0.398	-2.7 ± 55.9	0.911
Deposit-feeding clams	-14.8 ± 100.1	0.731	-20.6 ± 78.1	0.541

*Site D2, in the mid stratum, was highly influential in tests using biomass data and a potential outlier, so was omitted from the calculation.

Table 3. Results of paired analyses and tests for equality of variances (*F*-test) for estimates of species richness, evenness and diversity, between farm and reference sites

Index	Low stratum (d.f. = 6)		Mid stratum (d.f. = 6)	
	Mean difference (F–R) ± 95% CI	<i>P</i> -value	Mean difference (F–R) ± 95% CI	<i>P</i> -value
ACE	-1.5 ± 6.4	0.582	-1.8 ± 6.4	0.529
ICE	-2.1 ± 5.9	0.421	-3.3 ± 5.9	0.218
Jack-knife 1	-1.2 ± 5.1	0.595	-3.2 ± 5.1	0.180
Shannon–Wiener	-0.30 ± 0.37	0.103	-0.32 ± 0.37	0.082
Simpson’s evenness	-0.79 ± 1.31	0.192	-0.67 ± 1.31	0.257

details may have been poorly represented (Clarke 1993). Higher MDS stresses for biomass data (0.22, 0.23; Fig. 4) indicated a higher risk of misleading interpretations, although the stress was not high enough to indicate points were being placed at random. When *V. philippinarum* was removed from the analyses, the overall ordination changed little for density data (Fig. 3); *V. philippinarum* was highly influential in biomass data,

where its absence reduced the overall similarity among farm sites (Fig. 4).

ANOSIM tests found no significant differences in bivalve community composition between farm and reference sites, in any crossed analysis (Table 4). No significant differences were found for any factor considered (tide height, region, farming practices) with respect to biomass data. Significant differences among regions were apparent in the density data, regardless of the inclusion of *V. philippinarum* in the analysis. These regional differences were significant within reference sites but not within farm sites (Table 4).

Regional differences between communities were apparent within reference sites, but became less evident among the more similar farm sites. Although no differences in community similarity were observed between farm and reference sites, average pairwise similarity among farm sites was higher in every case but biomass data excluding *V. philippinarum* (Fig. 5). Excluding *V. philippinarum* from the data also reduced mean similarity within all groups.

The ratio of mean similarity from a species to the standard deviation of similarities within each group is a measure of how consistently that species contributes to the overall similarity within that group (Clarke 1993). For species contributing most to the similarity among farm sites, they also contributed more consistently than among reference sites (Table 5), which may account for the higher overall similarity between farm sites.

The seeded species *V. philippinarum* accounted for the largest component of the dissimilarity between farms and reference sites (see Table S2 in the supplementary material). There was no clear pattern regarding whether suspension feeders or facultative deposit feeders tended to be more abundant on farm sites.

Venerupis philippinarum also accounted for most of the dissimilarity between farm and reference sites by biomass data (see Table S3 in the supplementary material). Larger species contributed more to differences in biomass but were so numerically uncommon that they contributed very little in terms of density (see Table S2 in the supplementary material). The opposite was true for smaller, more abundant species. Not only were species such as *V. philippinarum*, *Protothaca staminea* and *Macoma inquinata* present in higher densities on farm sites, their biomass was also higher.

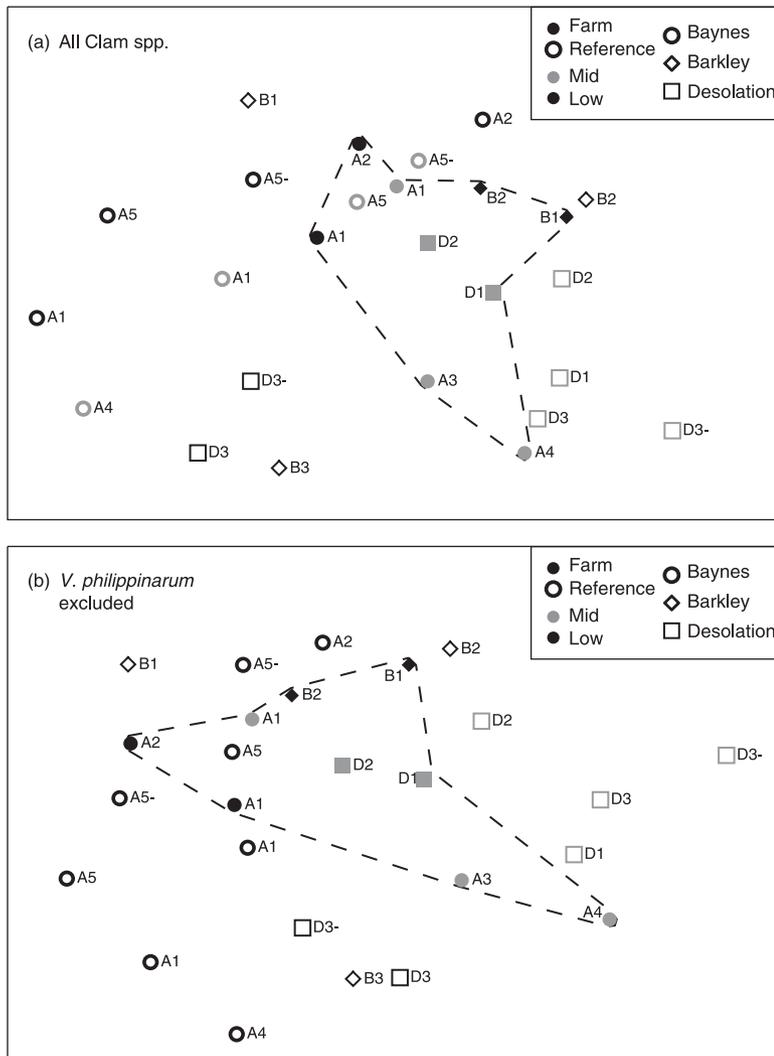


Fig. 3. (a, b) MDS plot of average density (individuals m⁻²) of clam species (a, stress = 0.18) and results of the same analysis with *V. philippinarum* excluded (b, stress = 0.19). Active farm sites have been outlined in a dashed line within the reduced ordination space.

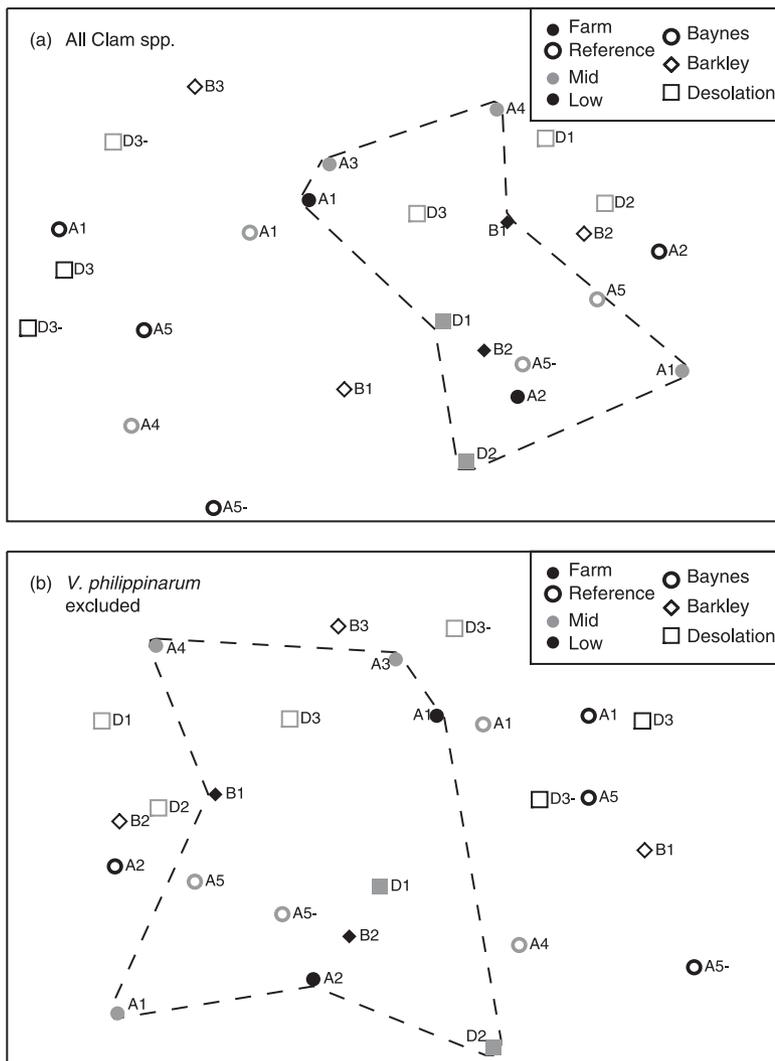


Fig. 4. (a, b) MDS plot of average biomass (g m^{-2}) of clam species (a, stress = 0.22) and the results of the same analysis with *V. philippinarum* excluded (b, stress = 0.23).

Discussion

Nets used for clam aquaculture are intended to reduce predator pressure on commercial species, and possibly

on other non-target species as an incidental side-effect. Clam seeding is intended to increase productivity of the commercial species. It can directly change the population dynamics of this species and possibly change the strength and form of interactions in intertidal communities. Increasing the density of a dominant filter-feeding bivalve can also increase rates of biodeposition and organic enrichment, thus indirectly affecting deposit feeders and altering community structure. If netting used in clam aquaculture reliably excludes clam predators, then overall densities are expected to be higher in areas of netting, in the absence of other limitations (Wilson 1990; Olafsson, Peterson & Ambrose 1994). Our results are not consistent with such a prediction.

Total bivalve density was significantly higher in farm sites compared with reference sites. This difference can be attributed to higher *V. philippinarum* densities on farm sites. Significant differences were only detected in the low stratum, which suggests that farming practices have the most consistent effects in lower intertidal areas, where there is a greater predation risk as well as increased feeding opportunities.

The BCSGA recommends seeding 200–400 clams m^{-2} , with an expected 40–50% loss prior to harvest (BCSGA 2004). This would account for an additional 100–200 individuals of commercial size m^{-2} before harvest. The sites used in this study were at various stages of harvest and seeding, with some recently harvested and others unharvested for several months. Nevertheless, on average, there were 227 more *V. philippinarum* m^{-2} on farms in the low stratum, which is close to the number expected as a result of seeding alone.

However, differences in density may also result from differences in natural recruitment. Adult *V. philippinarum* are harvested in BC after they are sexually mature, allowing them to broadcast spawn for at least one season. Netting has been shown to increase particle sedimentation (Spencer, Kaiser & Edwards 1996) and may also affect larval settlement, although this is presently unknown. Therefore, the relative contribution of seeding vs. larval settlement to densities on farm sites remains uncertain.

Table 4. ANOSIM results for bivalve community. Factors in two-way crossed analyses are listed with the crossed factor identified in parentheses. Statistically significant results are highlighted in bold

Factor (crossed with)	All clam spp.		<i>V. philippinarum</i> excluded	
	<i>R</i> -statistic	<i>P</i> -value	<i>R</i> -statistic	<i>P</i> -value
Density				
Farming practices (\times stratum)	–0.116	0.901	–0.199	0.989
Stratum (\times farming practices)	0.055	0.200	0.036	0.266
Farming practices (\times region)	–0.041	0.607	–0.115	0.840
Region (\times farming practices)	0.332	0.002	0.342	0.003
Region, farm only	0.146	0.235	0.028	0.431
Region, reference only	0.384	0.004	0.429	0.001
Biomass				
Farming practices (\times stratum)	–0.038	0.616	–0.043	0.643
Stratum (\times farming practices)	0.051	0.250	0.042	0.263
Farming practices (\times region)	0.024	0.397	0.009	0.461
Region (\times farming practices)	–0.045	0.662	–0.052	0.688

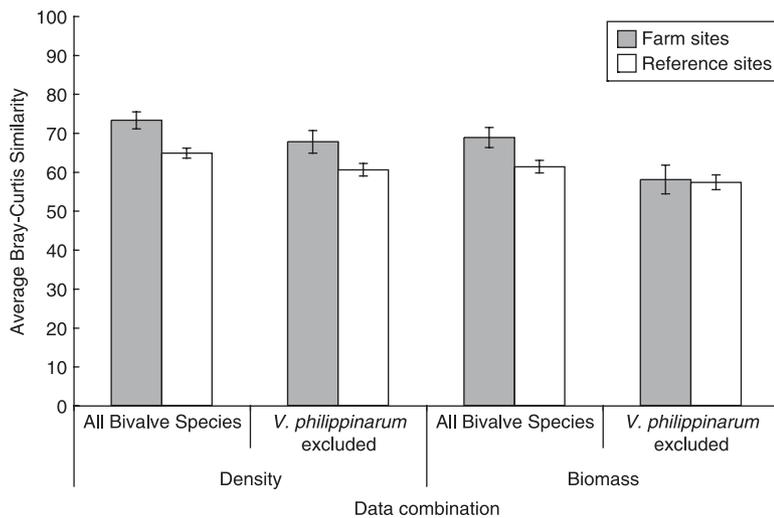


Fig. 5. Mean pairwise Bray–Curtis similarity (of fourth-root transformed data) within groups. Error bars show 95% confidence intervals about each mean.

Although *V. philippinarum* showed greater biomass on farm sites, total bivalve biomass did not increase significantly. The abundance of other bivalves, excluding *V. philippinarum*, was lower at farm sites on average, although not significantly different. Large confidence intervals indicate a low power to detect differences as large as 100 or more clams m^{-2} or 1000 or more $g\ m^{-2}$. Nevertheless, if *V. philippinarum* is increasing in abundance, yet total biomass is not significantly different, then other species may be less abundant on sites exposed to common aquaculture practices. This suggests that farm sites are dominated more by the commercial species than paired reference sites, which is also evident in abundance data from individual sites.

Other studies have found netting to be effective at increasing *V. philippinarum* survival (Spencer, Kaiser & Edwards 1997; Smith & Langdon 1998) but have not reported decreases in non-target faunal abundance, as suggested in our study.

CLAM HARVESTING

Nearly all unfarmed sites in our study areas are subject to recreational and commercial wild clam harvesting (Jamieson *et al.* 2001), performed using similar hand-raking methods as on farm sites, although perhaps at different frequencies. Brown & Wilson (1997) found that frequency did not affect the level of impacts from hand-raking. Clam harvesting using hand-rakes has been shown to mix sediment layers (Badino *et al.* 2004) and alter infaunal communities over the short-term, including reduced abundance and richness (Brown & Wilson 1997). Nevertheless, hand-raking of exposed areas during low tide is not likely to resuspend sediment, and the impacts are less severe than those reported from mechanical harvesting or dredging (Peterson, Summerson & Fegley 1987; Hall & Harding 1997; Spencer, Kaiser & Edwards 1997; Boese 2002).

Farm sites typically include clams at various stages of growth and, while not all farms are seeded every year, most farms are subjected to hand-raking at least once a year to harvest marketable clams. Because of the lack of unharvested reference sites, it was assumed in this study that the intensity of physical disturbance associated with bivalve harvesting was similar overall between farm and reference sites. The only exception was the D2 reference site, which was located in an area closed to shellfish harvesting, within 100 m of a public dock. High public traffic may have discouraged any form of harvesting, including poaching, in this area. This unusual site may provide an example of a bivalve community unaffected by anthropogenic bivalve removal.

PREDATOR EXCLUSION

It remains unclear why total bivalve densities, excluding *V. philippinarum*, appear to be unaffected by netting. Even if netting provides a refuge from predators, then space, food availability, nutrients or other unknown factors may limit populations to the current carrying capacity.

Table 5. Consistency of species' contributions to the similarities within farm and reference sites, by density. Species are listed in order of their contribution to the average similarity within the group. Bold values indicate higher consistency for that species than in the other group (farm/reference)

Farm		Reference	
Species	Average similarity/SD (similarity)	Species	Average similarity/SD (similarity)
Average similarity (%)	73.2		64.8
<i>Venerupis philippinarum</i>	6.42	<i>Venerupis philippinarum</i>	3.83
<i>Protothaca staminea</i>	3.81	<i>Protothaca staminea</i>	2.54
<i>Macoma balthica</i>	2.53	<i>Cryptomya californica</i>	2.63
<i>Cryptomya californica</i>	4.72	<i>Macoma balthica</i>	1.96
<i>Macoma inquinata</i>	1.66	<i>Mya arenaria</i>	2.11
<i>Macoma nasuta</i>	1.54	<i>Macoma inquinata</i>	2.28
<i>Mya arenaria</i>	1.66	<i>Macoma nasuta</i>	1.11
<i>Nuttallia obscurata</i>	0.77		

There is little evidence that space is a limiting resource in soft-bottomed sediments (Peterson 1979, 1992; Wilson 1990), and only 2% of available sediment volume was occupied by bivalves in the present study. The three-dimensional nature of sediments, and relative mobility of organisms, may offer opportunities to avoid direct competition, even in the absence of predation (Peterson 1979, 1992; Wilson 1990). Competitive exclusion is rarely observed and may not play an important role in structuring benthic marine communities in soft-bottomed habitats (Peterson 1979; Wilson 1990).

Alternatively, nets, as used in BC, do not effectively exclude epibenthic predators. Certain predators in the water column may be able to get under the nets when they are submerged by tides, as the edges are rarely buried (unlike Spencer, Edwards & Millican 1992) but secured to the substrate only at a few points. During our sampling, we occasionally found fish and crabs trapped under nets exposed by low tide. Crabs can be effective at limiting bivalve densities (Virnstein 1977; Smith & Langdon 1998) and may be able to forage under the netting in this study, thereby keeping bivalves at similar densities on both farm and reference sites. Many predators of benthic infauna are also themselves inhabitants of the sediment (Ambrose 1984) and cannot be excluded by surface netting. Infaunal predators may even benefit from epibenthic predator exclusion, leading to a shift in predator pressure on the benthic community without any change in overall mortality from predation (Gee *et al.* 1985). Given the evidence supporting the importance of predation in structuring soft-bottomed marine benthic communities (Peterson 1979; Wilson 1990; Olafsson, Peterson & Ambrose 1994), ineffective predator exclusion may account for the lack of differences observed in our results. The only natural predator reliably excluded by these nets may be large diving ducks (scoters *Melanitta* spp.).

Scoters may be responsible for the majority of clam disappearance at some sites, particularly in Baynes Sound (Lewis, Eslen & Boyd 2007), but little is known about how scoter predation is actually affected by nets. The BCSGA (2004) expects that as many as 40–50% of seeded *V. philippinarum* clams are lost from under nets at a typical clam farm before reaching harvest. Nevertheless, it is unknown whether clams are ‘lost’ to mortality by predators or if these clams simply move out from under the nets to other areas.

SITE DIFFERENCES

Multivariate community analysis revealed that bivalve composition among farm sites was more similar, on average, than among reference sites, reducing the regional separation evident among reference sites. The loss of ‘regional distinctness’ among farm sites appeared to be the result primarily of increased consistency in densities of common species at farm sites.

The conditions created by clam farming, which are intended to promote production of commercial

species, may create common pressures that drive separate communities towards higher levels of similarity. The homogenizing force of clam farming at large scales appears to be more significant than potential impacts at individual sites. The ability of common farming practices to alter habitat heterogeneity at smaller scales was not documented in this study, but is deserving of further research.

The large geographical scope of this study allowed us to observe differences in between-site variability previously undocumented in published studies of predator exclusion and clam farming. The implications of reducing interregional variation in community composition are unclear at this point, and offer an opportunity for further investigation and discussion. Several large-scale processes, including migration, settlement and resulting metapopulation dynamics may be affected by the spatial structure of habitat and communities themselves (Yu & Wilson 2001). Large areas of farming may interfere with source–sink population dynamics, possibly resulting in the loss of sink populations currently sustained through migration.

If clam farms become increasingly dominated by a single commercially valuable species, what are the implications for ecosystem processes performed by bivalves, such as nutrient cycling? It has been argued that if multiple species contribute to an ecosystem function, this can reduce variability in functional processes, as different species operate optimally under different environmental conditions (Yachi & Loreau 1999; McCann 2000; Emmerson *et al.* 2001). Species richness is often positively correlated with functional output (Emmerson *et al.* 2001; Tilman *et al.* 2001; Solan *et al.* 2004; Schläpfer, Pfisterer & Schmid 2005). On the other hand, a particular function may only require a single species to carry it out (Worm & Duffy 2003). Species-rich assemblages may simply have a greater chance of including a single highly active species that results in an overall high level of ecosystem function (Loreau 2000).

CONCLUSIONS AND RECOMMENDATIONS

Seeding and netting appear to affect bivalve communities at a regional spatial scale, larger than any single site in this study. If clam farming is a homogenizing force at large scales, then the greatest impact of clam aquaculture may result from cumulative impacts of several tenures within a given geographical area. The impacts of individual practices remain uncertain, as are the mechanisms underlying many of the results presented here.

Given the potential for unknown, large-scale cumulative impacts and the possibility for site-specific responses to farming practices, we recommend that regulatory efforts focus on baseline data collection, monitoring and site selection at a regional scale. Regulatory agencies responsible for site approvals are in a better position than individual lease owners to monitor and affect how aquaculture is distributed within regions.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from <http://www.blackwell-synergy.com>.

Figure S1. Map of study areas and site locations.

Figure S2. Clam and total shellfish aquaculture production in British Columbia (1990–2004).

Table S1. Values of diversity indices at each site.

Table S2. Species' contributions to farm and reference dissimilarity, by density.

Table S3. Species' contributions to farm and reference dissimilarity, by biomass.